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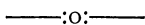
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bird, when it seized small mammals among the cactus beds, where they usually burrow for protection. One of the best unions, after gun-shot fracture, I ever had the pleasure of examining (the specimen is now in the Army Medical Museum), occurred, in the upper third of the humerus, in a specimen of *Mergus serrator*, that I secured several months ago. Taking into consideration the fact that this bird is a vigorous diver, and one of no mean powers of flight, the result, if we may so call it, was an excellent one—there being scarcely any deformity—and the member was as serviceable as ever.

I have seen and possess specimens of many other interesting cases, but their description would extend this paper far beyond the limits. The best examples, and those perhaps worthy at least of a mention, consist of a case of non-union in the palatines of *Anas boschus*, a depressed fracture in the cranium of *Corvus americanus*, gunshot injuries resulting in recovery of the brain in Spheotyto and others.



THE BRAIN OF THE LOCUST.¹

BY A. S. PACKARD, JR.

IN order to appreciate the habits, migratory, reproductive, &c., of the locust, and to learn something of its general intelligence as an insect and as compared with other insects, it is necessary for us to study with a good deal of care, the organ of the locust's *mind*, *i. e.*, its nervous system, comprising its nervous centers and the nerves arising from them.

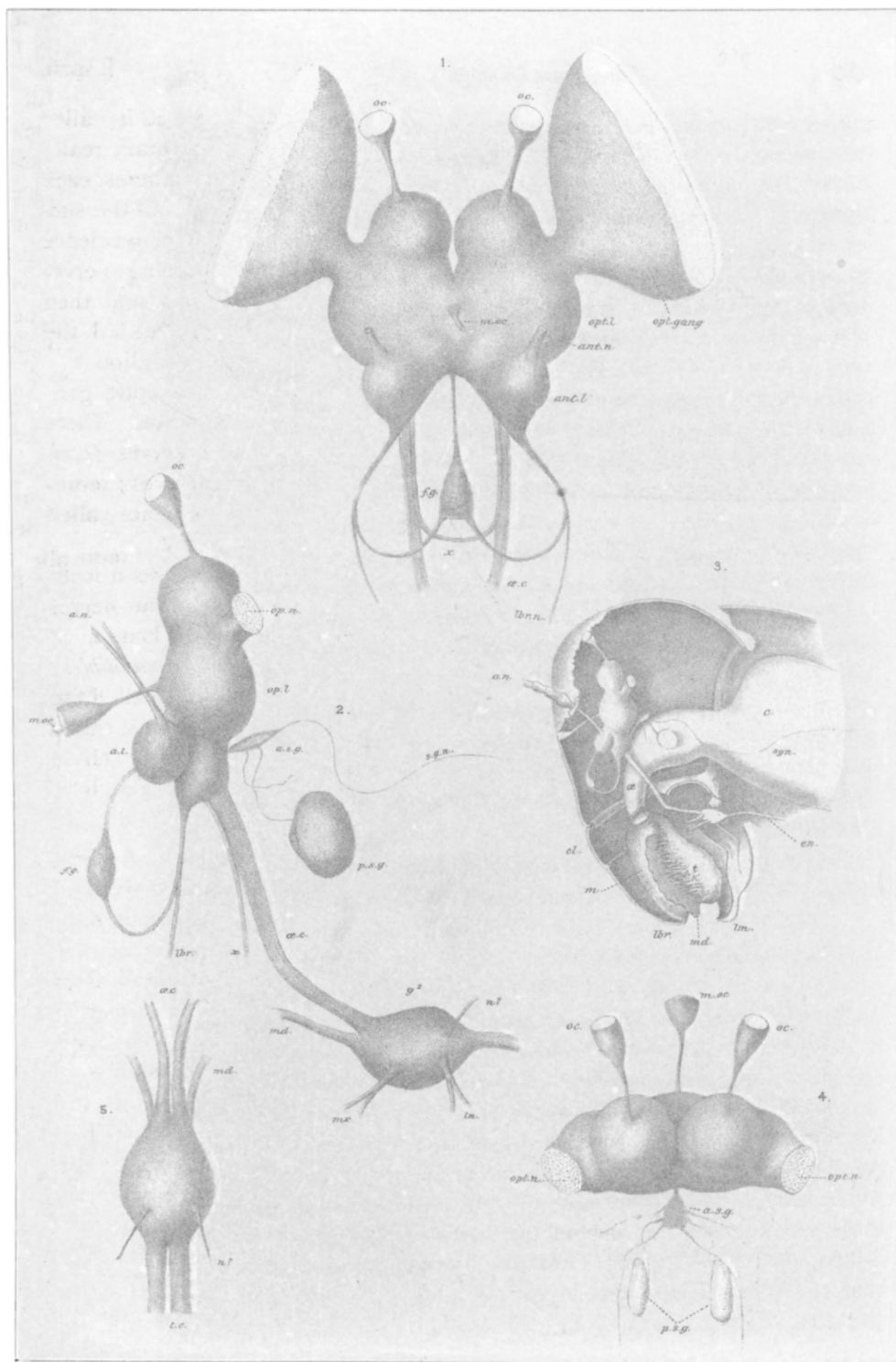
The Nervous System in General.—The nervous system of the locust consists of a series of nerve centers or *ganglia*, connected by nervous cords called *commissures*. There are ten of these ganglia in the locust, *i. e.*, two in the head, the first and largest of which is called the "*brain*;" three ganglia in the thorax, and five in the hind-body or abdomen. The brain is situated in the upper part of the head, resting upon the gullet or *œsophagus*, whence its true name *supraœsophageal ganglion*. (Plate I, Fig. 1.) The succeeding nerve-center is situated in the lower part of the head,

¹ Adapted for the NATURALIST from the Second Report of the U. S. Entomological Commission, 1880. We are indebted to the Commission for permission to have an edition of five plates struck off from the lithographic stones at the expense of the publishers

behind the mouth and under the œsophagus, hence it is called the *subœsophageal ganglion*. (Plate 1, Fig. 5.) The brain really is a double ganglion, being composed of two hemispheres, each hemisphere being a single ganglion or nerve-center; all the succeeding ganglia are also double ganglia; but for convenience we will call the "brain," and each of the succeeding nerve-centers a *ganglion*. Each side of the brain contracts, and then swells out into a rounded portion next to the eye, called the *optic ganglion*. (Pl. 1, Fig. 1.) From this optic ganglion the optic fibers proceed to the facets of the eye. The optic ganglion connects with the brain by the large optic nerve. There are, then, two *optic nerves*, besides three slender nerves (*ocellar nerves*) sent to each of the three *ocelli* or simple eyes; moreover, a nerve is sent to each of the antennæ, and are hence called the *antennal nerves*. The relations of the brain to the head, and to the succeeding ganglion, and the origins of the nerves distributed to the eyes, antennæ and ocelli, as well as of the nerves sent to the jaws, etc., are clearly seen in the figures on Plate 1.

On the other hand the mouth parts, *i. e.*, the jaws (*mandibles*) and accessory jaws (first and second *maxillæ*, the latter called the *labium* or under lip) are each supplied by a pair of nerves, called respectively the *mandibular*, *maxillary* and *labial* nerves. These three pairs of nerves arise from the subœsophageal ganglion. (See Pl. 1, Fig. 2, *g*².)

The Brain of Insects as distinguished from the Brain of Vertebrates.—The "brain," or supracœsophageal ganglion is, as we shall see, a much more complicated organ than any of the succeeding ganglia, having important parts which are wanting in all the others, hence it is *par excellence* nearer to our idea of a brain than any of the other nervous centers. It should be remembered, however, that the word, "brain" is applied to this compound ganglion simply by courtesy and as a matter of convenience, as it does not correspond to the brain of a vertebrate animal, the brain of the horse or man being composed of several distinct pairs of ganglia. Moreover, the brain and nervous cord of the fish or man are fundamentally different, or not homologous with those of the lower or invertebrate animals, though the nervous system of the insects and Crustacea present greater analogies to that of the vertebrates than any other of the lower animals, with the exception, perhaps, of the cuttlefish. The nervous cord of



the insect consists of a chain of ganglia connected by nerves or commissures, while the spinal cord of the fish or man is essentially "a double and fused series of nerve-centers." Moreover, if the vertebrate cord is cut through, a section shows that it consists of two kinds of substances or tissues, called the "gray" and "white" substance. The gray matter is situated in the center, and consists largely of nerve or so-called "ganglion cells," while the external white matter of the brain or cord is composed of a mass of nerve fibers. Now, in the nervous system of insects there is nothing to compare with these substances, but the ganglia, on the contrary, as we shall see farther on, consist primarily of an external layer of ganglion cells, whose fibers pass in to form a central fibrous mass or net-work, the meshes of which are filled with a fine granulated nerve substance, the nature of which is not clearly understood. Moreover, the entire brain of an insect is white, as are all the ganglia.

A ganglion in its simplest form is a little rounded mass, or nodule, of ganglion cells, with fibers leading from them: such cells are represented by Fig. 3*a*—3*e*, on Plate III. Now when the fibers lead in from the sensitive hairs on the crest of the insect, or from the antennæ, or the eyes or ears, and end in separate masses or lobes, which are modified ganglia, such ganglia are regarded as "sensory ganglia," and the nerves leading in from them are called ingoing or "afferent nerves," while the ganglia which give rise to the outgoing or "efferent" nerves, *i. e.*, those going to the muscles of the wings, legs, &c., are called "motor ganglia."

It should be borne in mind as the result of recent studies by several observers, as Leydig, Flögel, Dietl and Newton, that the subœsophageal ganglion, or "brain," of the insect is much more complex than any other ganglion, consisting more exclusively both of sensory as well as motor ganglia and their nerves. But it should also be understood that the subœsophageal ganglion also receives nerves of special sense, situated possibly on the palpi, and possibly on the tongue, at least the latter is the case with the bee; hence, this ganglion is probably complex, consisting of sensory and motor ganglia. The third thoracic ganglion is also, without doubt, a complex one, as in the locusts the auditory nerves pass into it from the ears, which are situated at the base of the abdomen. But in the green grasshoppers, such as the katydids and their

allies, whose ears are situated in their fore legs, the first thoracic ganglion is a complex one. In the cockroach and in the *Leptis* (*Chrysopila*), a common fly, the caudal appendages bear what are probably olfactory organs, and as these parts are undoubtedly supplied from the last abdominal ganglion, this is probably composed of sensory and motor ganglia; so that we have in the ganglionated cord of insects a series of brains, as it were, running from head to tail, and thus in a still stronger sense than in vertebrates the entire nervous system, and not the brain alone, is the organ of the *mind*, or psychological endowments, of the insect.

We will now proceed to examine the brain of the adult *Caloptenus spretus*, and compare it with that of other insects; then study its development in the embryo, and finally examine the changes it undergoes in the larva and pupal stages before attaining the fully developed structure of the adult locust.

Histological Elements of the Brain.—The brain is histologically or structurally divided into two kinds of tissue or cellular elements.

1. An outer, slightly darker, usually pale-grayish white portion is made up of "cortical cells," or "ganglion cells." (Pl. III., Fig. 3, *a*, *b*, *c*, *d*.)

This outer loose cellular envelope of the brain consists of large and small ganglion cells. Where the tissue consists of small ganglion cells, it is naturally from the denser arrangement of the smaller cells, which are packed closer together, rather darker than in those regions where the tissue consists of the more loosely disposed, large ganglion cells.

A. The large ganglion cells (Pl. III., Fig. 3, 3 *a*, 3 *b*, 3 *c*, 3 *d*, *e*) are oval, and send off usually a single nerve fiber; they have a thin fibrous cell wall, and the contents are finely granular. The nucleus is very large, often one-half the diameter of the entire cell, and is composed of large round refractive granules, usually concealing the nucleolus (the granules are much larger and fewer in number and the nucleolus is less distinct than in the brain of *Limulus*, the king crab). These large ganglion cells are most abundant and largest on each side of the upper furrow, and in front of the "central body," also at the bottom of the lower furrow, and along the exterior of the optic and antennal lobes, and along the commissural lobes.

B. The small ganglion cells apparently differ chiefly in size from the large ones, and are most numerous in the front swelling of each hemisphere; they surround and fill the calices of the mushroom bodies, and they extend along each optic nerve and form a large proportion of each optic ganglion, especially the layer next to the retina of the eye, though they are replaced by large ganglion cells at the junction of the fibrous part of the optic nerve with the dilated granular portion. The brain is surrounded more or less completely by the connective tissue cells belonging to the mesoderm or middle germ layer, and which are sometimes liable to be confounded with the ganglion cells, as they stain the same tint with carmine. It should be borne in mind that the nervous system, ganglia and nerves, originate from the tegumental or exodermal layer.

11. The medullary or inner part of the brain consists of matter which remains white or unstained after the preparation has remained thoroughly exposed to the action of the carmine. It consists of minute granules and interlacing fibers. The latter often forms a fine irregular net-work inclosing masses of finely granulated nerve matter.

In the antennal and commissural lobes is a third kind of matter, in addition to the granular and fibrous substances, which forms irregularly rounded masses, cream-colored in picro-carmine preparations, and which stain dark with osmic acid. This is called by Dietl "*marksubstanz*," and is described by Newton as "a peculiar arrangement of nervous matter, which appears sometimes as fine fibrillæ, with an axial arrangement, sometimes as a very fine net-work of different thicknesses, and sometimes as thin lamellæ, or altogether homogeneous."

It is to be noticed that this central unstained portion contains few, if any, ganglion cells, and it is most probable that the fibers of which it is composed originate from the cortical ganglion cells. At one or two points at Fig. 3, Pl. III, I have seen the fibers passing in from ganglion cells towards the middle of the brain. In the horseshoe crab (*Limulus*), owing to the simple structure of the brain, it is evident that the optic and ocellar nerves and posterior commissures originate from the large ganglion cells which in this animal are situated in or near the center of the brain. In the last abdominal ganglion also the fibers arising from the peripheral ganglion cells can very plainly be seen passing in towards

the center of the ganglion and mingling with the fibers forming it. Hence, in all probability the fibrous mass of the central part of the brain mostly originates from the peripheral or cortical ganglion cells.

To briefly describe the brain of the locust, it is a modified ganglion, but structurally entirely different from and far more complicated than the other ganglia of the nervous system. It possesses a "central body," and in each hemisphere a "mushroom body," optic lobe, and optic ganglion, and olfactory lobe, with their connecting and commissural nerve fibers, not found in the other ganglia. In the succeeding ganglia the lobes are, in general, motor; the fibers composing the œsophageal commissures, and which arise from the œsophageal commissural lobes, extend not only to the subœsophageal ganglion, but pass along through the succeeding ganglia to the last pair of abdominal nerve centers.¹ Since, then, there is a direct continuity in the fibers forming the two main longitudinal commissures of the nervous cord, and which originate in the brain, it seems to follow that the movements of the body are in large part directed or coördinated by the brain.² Still, however, a second brain, so to

¹ We have seen that the two great longitudinal commissures pass directly from the brain into and then pass backward from the subœsophageal ganglion, but beyond that point we have not traced their course, as it is generally supposed that they extend uninterruptedly to the last abdominal ganglia. This has indeed been shown to be the case by Michels, in his admirable treatise on the nervous system of a beetle (*Oryctes*) in Siebold and Kolliker's *Zeitschrift für wissen. Zoologie*, Band 34, Heft. 4, 1880. Michels states that each commissure is formed of three parallel bundles of elementary nerve fibers, which pass continuously from one end of the ventral or nervous cord to the other. "The commissures take their origin neither out of a central punctsubstanz (or marksubstanz), nor from the peripheral ganglion cells of the several ganglia, but are mere continuations of the longitudinal fibers which decrease posteriorly in thickness, and extend anteriorly through the commissures forming the œsophageal ring to the brain."

² The following extract from Newton's paper shows, however, that the infra or subœsophageal ganglion, according to Faivre, has the power of coördinating the movements of the body; still it seems to us that the brain may be primarily concerned in the exercise of this power, as the nerves from the subœsophageal ganglion supply only the mouth parts. "The physiological experiments of Faivre, in 1857 (*Ann. J. Sci. Nat.*, Tom. viii. p. 245), upon the brain of *Dytiscus* in relation to locomotion, are of very considerable interest, showing, as they appear to do, that the power of coördinating the movements of the body is lodged in the infraœsophageal ganglion. And such being the case, both the upper and lower pairs of ganglia ought to be regarded as forming parts of the insect's brain." *Quart. Jour. Micr. Sc.*, 1879, p. 342.

speak, is found in the third thoracic ganglion of the locust, which receives the auditory nerves from the ears situated in the base of the abdomen; or in the first thoracic ganglion of the green grasshoppers (katyids, &c.), whose ears are in their fore legs; while even the last abdominal ganglion in the cockroach and mole cricket is, so to speak, a secondary brain, since it receives sensory nerves from the caudal stylets which are provided with sense organs.

*Description of the sections of the Brain.*¹—We will now describe the sections upon which the subsequent account of the brain is founded. The sections, unless otherwise stated, are *frontal*, i. e., cut transversely across the face from before backwards; in cutting thus through the head, twelve sections were made before the front part of the brain was touched, the thirteenth grazing the front of the brain. Section fourteen passed through the anterior part of both *calices*, but did not touch the stalk of the *mushroom body* (these terms will be explained farther on). It passed through the central region of each hemisphere, including the front part of the *trabeculæ* or base of the stalk of the mushroom body. The section passed through the commissural lobes, the lower third being composed of the ganglion cells, but the substance of the commissure itself is filled with the ball-like masses of "marksubstanz." The commissures to the subœsophageal ganglion were not touched, and do not appear in the section, since they arise from the back of the brain.

In section 15 no additional organs are exposed. In section 16 (Pl. II, Fig. 1) the trabeculæ are seen, when magnified 225 diameters, to be composed of ascending fibers, which form the base or origin of the double stalk of the mushroom body.

Section 17 (Pl. II, Fig. 2) is the most important of all the sections, as the entire mushroom body and the central body are cut through, together with the antennal lobes, and the commissural lobes, and also the origin of the optic nerves.

In section 18 (Pl. II, Fig. 4) the double nature of the stalk of the mushroom body is seen; the optic lobes are now well marked, and the razor grazed the back of the commissural lobes, as well as the inner side of the optic ganglion. The section passed behind the trabeculæ and the base of the stalk and through the back of

¹ We are indebted to Mr. Norman N. Mason, of Providence, R. I., for cutting and mounting the sections used in making the observations here recorded.

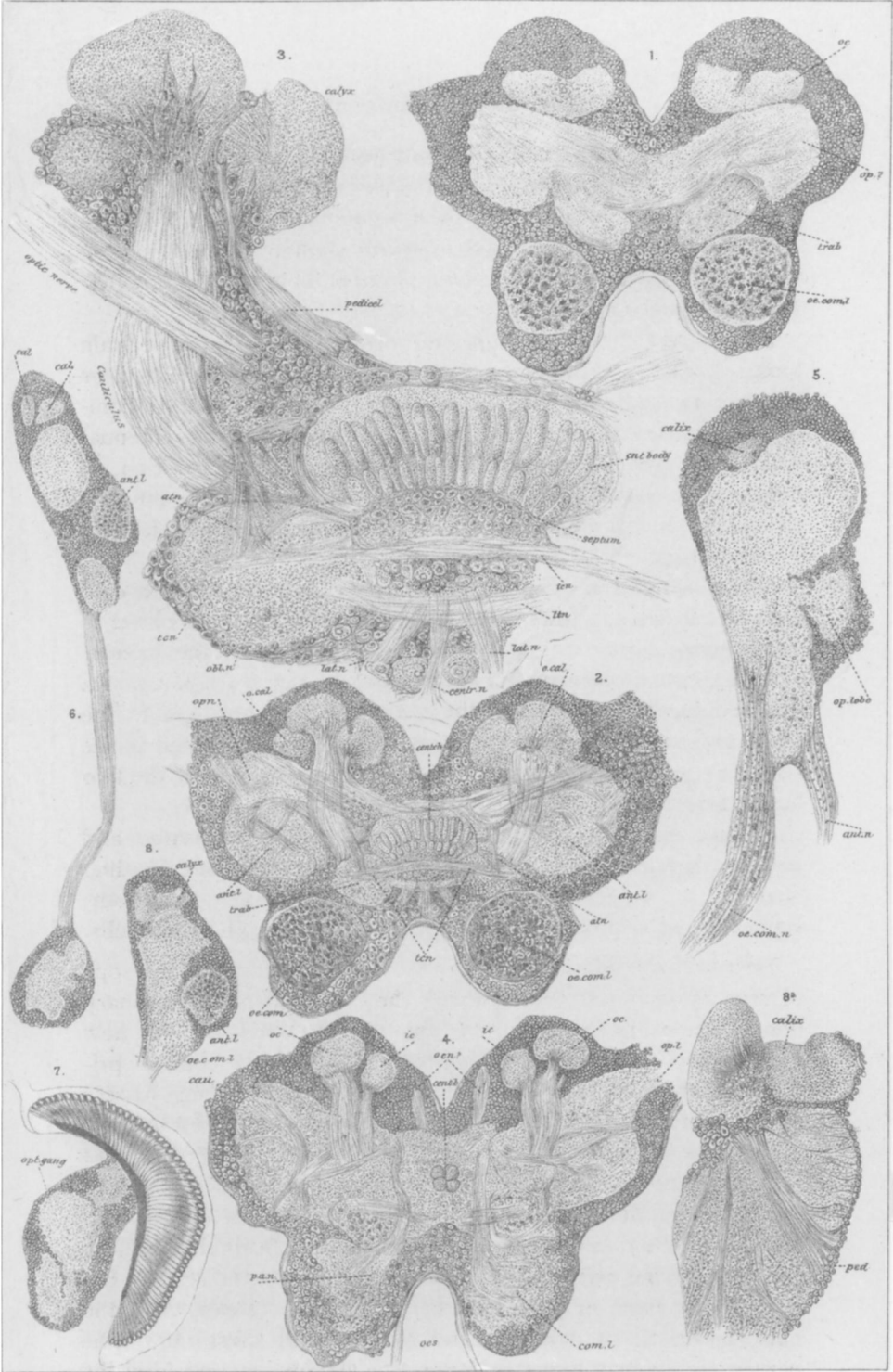
the central body. The calices are each seen to be so furrowed and uneven as to appear in the section as two separate portions. Two important nerves (Pl. II, Fig. 4, *p. a. n.*) are seen to arise from the commissural lobes, and to pass upwards, ending on each side of the upper furrow, near the origin of what we think are possibly the ocellar nerves (*o. c. n. ?*).

Section 19 (Pl. III, Fig. 1) passed through the back of the brain (compare Fig. 4, of the same plate, which represents a vertical or longitudinal section of the brain), through the œsophageal commissures, and the back edge of the calices, while the antennal lobes and a part of the optic lobes are well seen in the section. A transverse commissural nerve (*t c n*) connects the two antennal lobes, and the commissural nerves are seen to cross at the bottom of the furrow.

Section 20 (Pl. III, Fig. 2), which passes through the extreme back of the brain, shows in this plane four transverse bundles of nerve fibers connecting the two hemispheres, *i. e.*, the inferior (*inf. n.*), two median (*m. n.*) and a superior nerve (*sup. n.*). In this section the relations of the optic ganglion and eye to the brain are clearly seen, the optic ganglion being situated in the posterior region of the brain. It will also be seen that the two hemispheres are at this point only connected anteriorly.

In sections 22, 23 and 24 the brain nearly disappeared, and only the optic ganglia were cut through by the microtome, affording instructive sections of the three lenticular masses of white unstained granulo-fibrous substance surrounded by ganglion cells.

Internal Topography of the Brain.—Disregarding the envelope of cortical ganglionic cells, though they are evidently of primary importance in the physiology of the insect's brain, we will now describe the internal topography of the brain. It consists primarily of an irregular net-work of nerve-fibers, inclosing masses of granulated nerve matter. This mass is divided into a number of separate areas or lobes, of which the "central body" (*corpus centrale* of Flögel and Newton) is single and situated between or in the median line of the two hemispheres. There is also a primitive superior and inferior central region, better shown, however, in the brain of the embryo and larval locust than in the adult. Besides these areas are the rounded masses or "lobes," *i. e.*, the optic, antennal, or olfactory and commissural lobes; the optic nerves arising from the optic lobes, the antennal nerves from the



A.S. Packard, del.

A. Meissl lith. Boston.

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antennal lobes, and the commissures surrounding the œsophagus and connecting the brain with the subœsophageal ganglion, and which arise from the commissural lobes. Finally a "mushroom body" is situated in the upper and central part of each hemisphere.

The Central Body.—This is the only single or unpaired organ in the brain. It is best seen in section 17 (Pl. II, Fig. 2), which also passes through the optic and antennal lobes and the trabeculæ and mushroom bodies. This singular organ is apparently present in all winged insects, though differing somewhat in structure in different insects. It is, as seen in Pl. II, Fig. 2, situated in the same plane as the peduncle and in the same plane as the center of the entire mushroom body, and rests upon the inner sides of the trabeculæ. Section 16 does not pass through it, though the next section, which is $\frac{1}{500}$ inch thick, passes through its middle. Section 18 (Fig. 4) passes through its back, while the next section does not include any part of it; hence its antero-posterior diameter is slightly over $\frac{1}{500}$ of an inch. It is about twice as broad as high, and thus is a small body, though from the universality of its occurrence in winged insects, it may be one of considerable importance.

It is surrounded by a dense net-work of fibers containing a few small ganglionic cells, the fibers in front continuous with those near the bottom of the frontal median furrow and connecting the two optic lobes. Posteriorly the fibers apparently are not continuous with those of the trabeculæ; hence the central body appears to be quite isolated from the rest of the brain. Its substance, when magnified 400 diameters, appears to be a white granular matter like the adjoining parts of the brain. It is divided into two parts, the superior and inferior, the former part constituting the larger part of the body. The inferior portion is separated by fibers from the superior; it contains numerous nucleated spherical cells situated either irregularly or perhaps primarily (see Pl. IV, Fig. 3, of the pupa) in two rows when fewer in number than in the adult. The superior and larger division of the central body contains two series of what we may call *unicellular bodies*, sixteen in a series. The lower series are spherical or slightly elongated, and rest in the fibrous partition or septum, forming the floor of the superior division of the central body. The upper row of bodies are cylindrical, and about three or four times as

long as thick. They are separated by thin fibrous septa. Pl. iv, Fig. 2, represents the central body enlarged 225 diameters. When we examine the central body in an earlier stage, *i. e.*, the second pupal (Pl. iv, Fig. 3), we see that the body is covered above by a stratum of nucleated ganglion cells continuous with those next to the bottom of the upper furrow; and that the fibrous septum between the upper and lower division also contains small cells. These cells disappear in the adult, and evidently give rise to the fibers which take their place. It will also be seen that the "unicellular bodies" are shorter, more cell-like than in the adult; hence they seem to be modified ganglion cells, which have at an early date lost their nucleus and nucleolus. My observations on the central body of the locust agree in the main with those of Newton (compare his Fig. 9). His drawings are not especially clear and definite, but the differences appear to be unimportant. There are perhaps two (16 instead of "12 or 14") more cellular bodies in the locust than in the cockroach. Unfortunately my sections of the brain of the cockroach do not show the central body. Dietl states that the central body is a "median commissural system." This description we would accept in a modified sense. We have shown that the unicellular bodies and the cells beneath them were once like the ganglion cells, but that they have lost their nuclei and nucleoli; hence the functions of the central body must be unlike that of an ordinary commissural lobe. Flögel states that the number of "sections," or what I call unicellular bodies, is eight; we have counted sixteen. Both Flögel and Newton appear to regard these bodies as simply spaces or sections between fibrous partitions; but it would appear that these sections are really modified cells, and that the fibrous septa are possibly the cell-walls, somewhat modified.

The Mushroom Bodies.—These curious organs have attracted a good deal of attention from writers on the brain of insects. Dujardin, in 1850, first drew attention to them. His memoir we have not at hand to refer to, but as stated by Newton¹—

"Dujardin pointed out that in some insects there were to be seen upon the upper part of the brain certain convoluted portions which he compared to the convolutions of the mammalian brain, and, inasmuch as they seemed to be more developed in those insects which are remarkable for their intelligence, such as ants,

¹ On the Brain of the Cockroach. By E. T. Newton. Quart. Journ. Microscopical Science, July, 1879, pp. 341, 342.

bees, wasps, &c., he seemed to think the intelligence of insects stood in direct relationship to the development of these bodies. The form of these structures is described by the same author as being, when fully developed, as in the bee, like a pair of disks upon each side, each disk being folded together and bent downwards before and behind, its border being thickened and the inner portion radiated. By very careful dissection he found these bodies to be connected on each side with a short pedicle, which bifurcates below to end in two tubercles. One of these tubercles is directed towards the middle line, and approaches but does not touch the corresponding process of the opposite side. The second tubercle is directed forwards, and is in close relation to the front wall of the head, being only covered by the pia mater (neurilemma). These convoluted bodies and the stalks upon which they are mounted are compared by Dujardin to certain kinds of mushrooms, and this idea has been retained by more recent writers on the subject."

The form of the mushroom body is much more complicated in the bee or ant than in insects of other orders. In the cockroach and in other Orthoptera, notably the locust, the four divisions of the calices are united into two; while the structure of the calyx in the cockroach is quite different from that of the locust. Mr. Newton, in his description, notwithstanding Dujardin's statement, appears to practically limit the term "mushroom body" to the cap or calyx on the end of the stalk. In the following description we apply the term "mushroom body" to the entire structure, including the base or trabecula, the double stalk, and the cap or calyx.

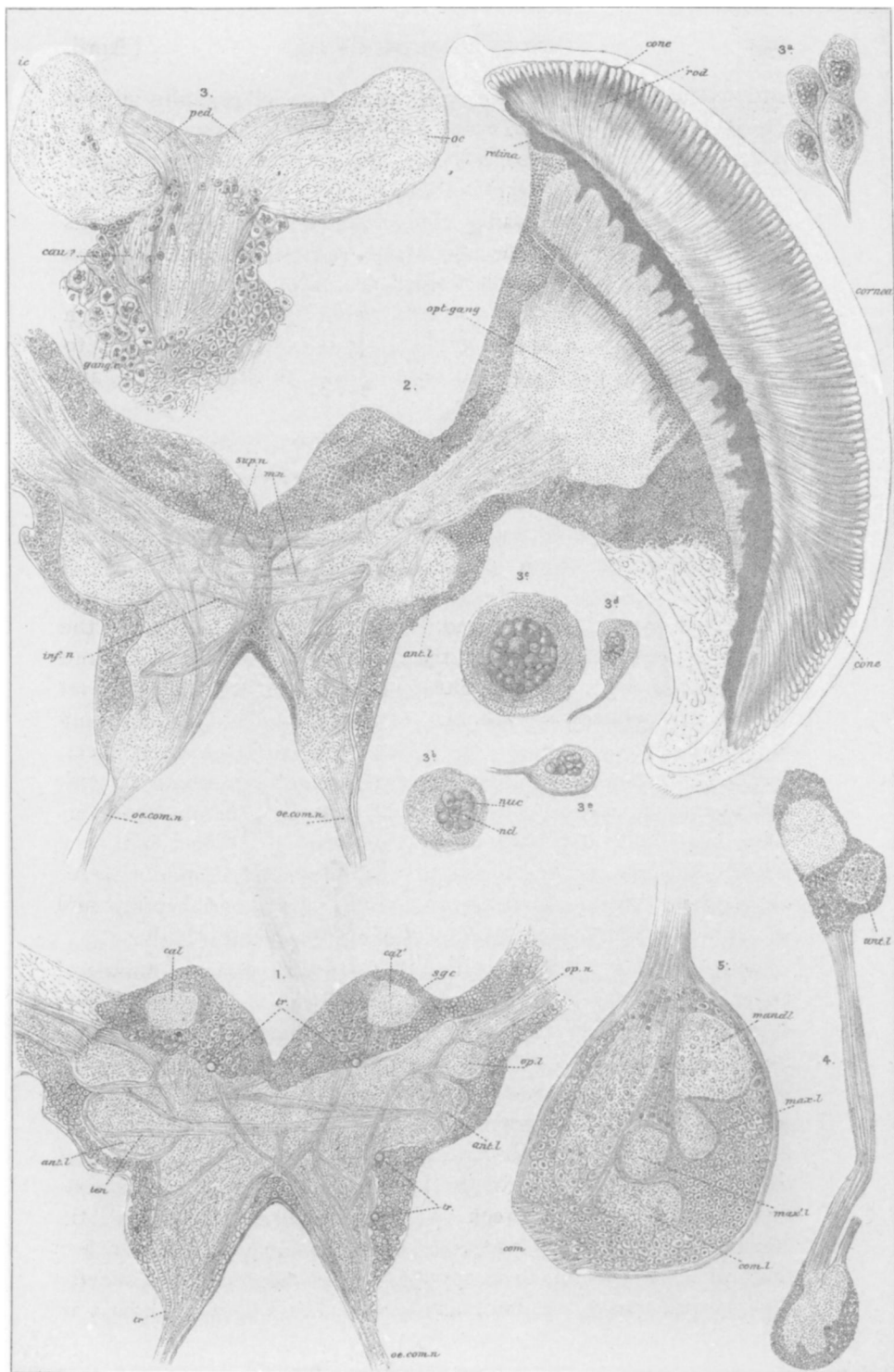
So far as we have been able to observe, the double stalk of the mushroom body rests on a rounded mass of granulo-fibrous nerve matter; this rounded mass or base of the column is called the *trabecula* (Pl. II., Fig. 2, *trab.*). The two *trabeculæ* (one in each hemisphere) are much more widely separated (in my sections) than in the cockroach or in those insects studied by Flögel; the space between them being filled by a loose cellular mass containing small nucleated cells. The thickness of each *trabecula* is greater than that of the double stalk. Section 14 passes through the outer or anterior edge of the *trabecula*, and also through the calices at some distance from the edge. Section 18 (Fig. 4) does not include it, though showing well the mushroom body, with the exception of the base of the double stalk. It follows that the thickness of the *trabecula* is about $\frac{3}{800}$ of an inch.

The substance of the *trabecula* is seen to be minutely fibrous

under a power of 725 diameters, with masses of granules among the fibers which are much finer than in the optic or antennal lobes. At the point passed through by section 17 the trabeculæ appear to have no connection with the stalk, but the latter appear to stop abruptly just before reaching it, the envelope of ganglionic cells and fibers surrounding the trabeculæ being interposed between the base of the stalk and the trabecula. (This does not preclude the fact that the stalk does not arise from the trabecula, though there are no signs of it in this section; for it clearly appears to thus arise in the drawings and descriptions of Dietl, Flögel, and Newton.)

The structure of the trabeculæ in the locust, judging from our sections, appears to be more complex than would be inferred from the observations of the other anatomists just mentioned. Section 17 (Pl. II., Fig. 2, *trab.*) passes through the middle of each of these bodies, and it then appears that there are four bundles of nerve-fibers passing out of each body. A bundle of transverse nerve-fibers (Fig. 2, *t. c. n.* and Fig. 3) passes along under the central body, directly through the middle of the trabeculæ, and anastomoses with the fibrous envelope of each trabecula. In front of this transverse intra-trabecular nerve is a small short ascending bundle of fibers (Fig. 3 *a. t. n.*) which passes next to the pedicel, but does not apparently form a part of it, but anastomoses with the fibers on each side of the central body. Below, the fibers pass downward and outward to apparently connect with the fibrous envelope of the trabecula. Another short bundle passes out from the trabecula obliquely towards the central body and anastomoses with the fibrous envelope of the central body.

Below, but in the same plane, is another transverse bundle of fibers (Fig. 3, *l. t. n.*), which is slightly curved and on the left side its fibers are distinctly seen to enter the trabecula. This lower intra-trabecular nerve, as we may call it, connects with three vertical short nerves arising from near the edge of the lower furrow between the hemispheres of the brain. Of these, the central one (*centr. n.*) is in the median line of the brain, and the lateral ones (*lat. n.*) are on each side. There would thus seem to be a direct double nervous communication between the two trabeculæ, and with the fibers surrounding the central body, and hence with the rest of the brain. This seems to be opposed to the statement of Newton that the trabeculæ, and the mushroom bodies in general, have no



A.S. Packard, d.d.

A. Mead lith. Boston.

nervous connection with the rest of the brain. This section also clearly indicates the origin of the optic nerve, which passes *behind* the stalk of the mushroom body, and also the relation of the fibers of the stalk to the calices, as they appear to penetrate far into the interior of the body of each calyx.

The Double Stalk (cauliculus and peduncle).—These names are applied to the larger and smaller divisions of the stalk of the "mushroom body." They are represented in the eighteenth section (Fig. 4) where the outer part of the stalk (*cauliculus*) supports the outer calyx, and the inner slenderer column of fibers supports or ends in the inner division of the calyx. These two bundles of fibers are somewhat curved, but as they do not appear in sections 16 and 19, must be less than $\frac{3}{8}$ of an inch thick. Their fibers are seen to penetrate deeply into the base of the calices, and thus to directly communicate with the fine granular substance of the calices.

The Calices.—The cups of the mushroom bodies in the locust differ decidedly in form from those of the cockroach, and this part of the mushroom body is more variable in form in the different orders of insects than any of the other parts of the brain. It is nearly obsolete, or, as Flögel states, "not more than rudimentary" in hemipterous insects (notably *Syromastes*), and is less completely developed in many smaller moths, beetles, and flies, as well as Neuroptera (*Æschna*), according to Flögel, than in the larger moths, in the Orthoptera, and especially in the Hymenoptera, where it is well developed. We have been unable to find it as yet in the brain of myriopods or of the spider. In the locust each body is more or less rounded and rudely saucer-like rather than cup-like, with the rim very thick; the hollow of the cup, if it be hollow, is small in proportion to the thickness of the saucer-like cup. The diameter of a calyx is about $\frac{3}{8}$. The anterior edge reaches to the front edge of each hemisphere of the brain, but does not extend to the back part of the brain. The relations in a vertical, *i. e.*, longitudinal section of the mushroom body to the rest of the brain are seen in Pl. II, Fig. 8 *a*. It thus appears that the double stalk is situated near the center of the brain, and that the cup projects far forward, but posteriorly does not extend behind the antennal lobes or the commissures. In section 18 (Fig. 4) the calices are seen to be double, the outer (*o. cal.*) attached to the cauliculus (*cau.*) and the inner arising from the peduncle

Fig. 8 *a* gives an idea of two calices and their mode of attachment to the stalk. The peduncle (if we interpret that division of the stalk aright) sub-divides, sending a thick bundle of fibers to each calyx, ending abruptly in the hollow of the calyx. The substance of the calices is finely granular, with some coarse granules, and apparently short scattered irregular fibers. The structure of the calices of the locust appears to be more homogeneous than that of the cockroach, judging by our sections of the latter. Owing to different treatment by reagents the dark masses described by Newton as existing in the cockroach were not so clearly shown in my sections ($\frac{1}{1000}$ inch thick) as in those made by Mr. Newton. The substance of the calices when examined under a power of 725 diameters is much the same both in the cockroach and the locust, the dark bodies not appearing in either. The form of the calices is very different in the cockroach, the calices being truly cup-like, the disk being deeply folded, and the edges of each cup being thin compared with those of the locust.

The Optic Lobes.—As seen in section 19 (Pl. III, Fig. 1 *op. l.*) these bodies are larger than the antennal lobes, and consist of numerous irregular small bundles of fibers besides those composing the optic nerve, the interspaces being filled with fine granular nerve substance. The optic nerve is much larger at the outer edge of the lobe before passing into the optic ganglion, the fibers still being immersed in the finely granular nervous substance.

The Optic Ganglion.—This is situated at the back of the brain, and is a large rounded mass of white fine granular nervous matter, enveloped in very numerous but small ganglion cells, which stain dark red by carmine, the granular matter remaining unstained by the picrocarmine. The granular or white portion is subdivided into three rudely lens-shaped masses (see Pl. v, Fig. 1), the one nearest the eye being much the largest.

The Antennal or Olfactory Lobes.—Section 19. (Pl. III., Fig. 1, *ant. l.*). These are smaller than the optic lobes, though in section 19 they appear larger. They give rise to the antennal nerve, and as the locust carries its ears at the base of the abdomen, the auditory nerves entering the third thoracic ganglion, reasoning by exclusion the antennæ in Orthoptera must be organs of smell, and the lobes and nerves to the antennæ are consequently olfactory. This is the opinion of some recent writers, notably Hauser.¹

¹ Physiologische und histologische Untersuchungen über das Geruchsorgan der Insekten. Siebold und Kölliker's Zeitschrift für Wissen. Zoologie, Bd. 34, Heft. 3.

The lobes are, as described by the other observers, filled with ball-like yellowish masses, which stain dark by osmic acid, much as in the commissural lobes. Nerve fibers are seen in section 19 to pass from one antennal lobe to the other in the rear of the central body and of the trabeculæ, while other nerve fibers are seen to pass into the optic lobes and the commissural lobes. This system of intra-lobe nerves demonstrates that there is a nervous intercommunication between these cerebral lobes and the ganglionic chain of the entire body.

The Commissural Lobes.—From these large bodies proceed the two great longitudinal commissural nerves, forming the connecting threads of the nervous cord, and which extend from the brain to the last abdominal ganglion, passing through the intermediate nerve centers. The lobes are filled with ball-like masses, of the same general appearance as in the antennal lobes, but more distinct and numerous.

Comparison of the Brain of the Locust with that of other insects.—Newton rightly regards the cockroach's brain as a generalized form of brain, which may serve as a standard of comparison. The cockroach is geologically one of the oldest of insects; its external and internal structure is on a generalized plan, and the brain conforms to this order of things. Our knowledge of the cockroach's brain is derived from the photographs and account of Flögel, and Newton's excellent descriptions and figures, supplemented by two sets of sections made for us by Mr. Mason, but which unfortunately, are quite defective as regards the trabeculæ and stalk of the mushroom body. The shape of the calices of the cockroach, as already stated, is very different from that of these bodies in the locust, and indeed from any other insect yet examined, the cup being very deep and the sides thin; but the intimate structure seems nearly the same in the two insects.

In the cockroach the antennal and commissural lobes are of much looser texture, with large and numerous ball-like masses (*ballensubstanz*); these are, when magnified 400 diameters, not only larger, but more distinct from the rest of the nervous matter of the lobe than in the locust. When magnified, as mentioned, the ball-like masses appear to be simple masses of finely granular nervous matter, with darker granules, much like the rest of the granular portions of the brain, but with coarser granular masses than in the substance of the optic lobes. These ball-like masses

are surrounded by a loose net-work of anastomosing nerve fibers continuous with those of the antennal nerve, and with scattered nucleated cells, which become very numerous in the antennal nerve. The nerve fibers are stained reddish by the picrocarmine.

Turning now to other orthopterous insects, Flögel mentions Acrydium, but states that he had no serviceable preparations, and after describing the brain of Forficula, the ear-wig, says: "As I observe in Acrydium, the cells and fibers in this animal are especially large, and these objects invite further investigation." Flögel's photograph and description of the brain of Forficula, a representative of an aberrant family of Orthoptera, and Dietl's beautiful figures and descriptions of the brain of the molecricket (*Gryllotalpa vulgaris*) and the cricket (*Acheta campestris*), show that the orthopterous brain, judging from these representative forms, is constructed on a common type, the most variable part being the calices of the mushroom body.

From these facts we should judge that, on the whole, the locusts were as highly endowed intellectually as any other insects, with the exception of the ants, bees, or wasps, *i. e.*, the social species; for in these forms the insect brain reaches its highest development, as we might expect from the wonderful instincts and power of reasoning exhibited by these social species; while in a number of insects the brain is less developed than in the locust. It would thus appear that, as in the vertebrates, there are different grades of brain-development, considerable extremes existing in the same sub-class of insects, as for example, in the same sub-class of mammals.

The brain of the bee and ant, as shown by Dujardin and demonstrated by Dietl and Flögel, is constructed on a higher, more complicated type than in the other winged insects, owing to the much greater complexity of the folds of the calices or folded disk-like bodies capping the double stalk of this organ.

[To be concluded.]

LETTERING OF THE FIGURES ON PLATES I—V.

centr. b., central body.

trab., trabecula.

cau., cauliculus.

ped., peduncle.

o. cal., outer calyx, or cup.

i. cal., inner calyx.

op. l., optic lobe.

op. n., optic nerve.

ant. l., antennal lobe.

ant. n., antennal nerve.

æ. com. l., œsophageal commissural lobe.

æ. com. n., œsophageal commissural nerve.

æ. c., œsophageal commissural nerve.

lbr. n., nerve to labrum.

l. g. c., large ganglion cells.

s. g. c., small ganglion cells.

opt. gang., optic ganglion.

sg. n., sympathetic nerve.

t. n., transverse nerve.

u. intr. n., upper intratrabecular nerve.

l. intr. n., lower intratrabecular nerve.

ln., nerve to labium.

fg., frontal ganglion.

psg., posterior sympathetic ganglion.

lat. n., lateral nerve.

centr. n., central nerve.

obl. tr. n., oblique trabecular nerve.

a. t. n., ascending trabecular nerve.

m. n., two median commissural nerves.

sup. n., superior commissural nerve.

in. n., inferior commissural nerve.

tr., trachea.

up. l., upper cerebral lobe of embryo.

low. l., lower cerebral lobe of embryo.

gang. c., ganglion cells.

gran., granules of the central nervous matter.

æs., œsophagus.

int., integument.

o. n., ocellar nerve; *oc.*, ocellus.

n. c., ventral nervous cord.

ncl., nucleolus.

lbr., labrum.

md., mandible.

lm., labium.

cl., clypeus.

EXPLANATION OF PLATE I.

FIG. 1.—Front view of the brain of *Caloptenus femur-rubrum*.

FIG. 2.—Side view of the same.

FIG. 3.—Side view of the head showing the relation of the brain to the mouth (*m*) and œsophagus (*æ*) and walls of the head.

FIG. 4.—The brain as seen from above, and the three ocelli.

FIG. 5.—The subœsophageal ganglion seen from above. Drawn by E. Burgess.

DESCRIPTION OF PLATE II.

FIG. 1.—Frontal section 16, through the front of the brain of adult *Caloptenus spre-tus*; $\times \frac{1}{2}$ inch objective, A. eye-piece.

FIG. 2.—Section 17, showing the central body (*centr. b.*) and mushroom body, optic and antennal lobes, and commissural lobes; $\times \frac{1}{2}$ A.

FIG. 3.—Enlarged view of the trabecula and its nerves, of the mushroom body, its calices and stalk, and the origin of the optic nerves; $\times \frac{1}{3}$ A., 225 diameters.

FIG. 4.—Section 18, passing through the back of the central body, showing the double nature of the stalk of the mushroom body, and passing through the back of the commissural lobes and behind the trabecula and the base of the stalk; $\times \frac{1}{2}$ A. Are *oc. n.* ? the origins of the ocellar nerves?

FIG. 5.—Vertical (longitudinal) section through one of the hemispheres, showing the origin of the commissural and antennal nerves and the optic lobe.

FIG. 6.—Longitudinal section through the brain and subœsophageal ganglion ($\times 50$ diameters), showing the two portions of the calyx, the antennal lobe, and in the subœsophageal ganglion the three lobes giving off respectively the mandibular, maxillary, and labial nerves.

- FIG. 7.—Longitudinal section through the optic ganglion and the eye; $\times 50$ diameters.
- FIG. 8.—Longitudinal section through the brain, showing the calyx, antennal lobes, and commissural lobes; $\times 50$ diameters.
- FIG. 8 a.—Enlarged view of Fig. 8 ($\times \frac{1}{2}$ B.), showing the relations in a longitudinal section of the calyx to the stalk, although the direct connection of the stalk with the calyx is not seen in this section.

DESCRIPTION OF PLATE III.

- FIG. 1.—Section 19 ($\times \frac{1}{2}$ A), passing through the back of the brain, showing the posterior edge of the calices and antennal lobes and oesophageal commissural nerves and optic nerve. *tr.*, small tracheæ.
- FIG. 2.—Section 20, passing through the back of the brain, showing the relation of the optic nerve to the optic ganglion and eye; the cornea, cones, rods and retina of the eye are shown; $\times \frac{1}{2}$ A. *sup. n.*, superior, *m. n.*, median, and *inf. n.*, inferior commissural nerves connecting the hemispheres.
- FIG. 3.—Enlarged view of upper part of the stalk and calyx, and the ganglion cells surrounding and filling the latter; $\times 225$ diameters. 3 *a, b, c, d*, different ganglion cells seen from different directions, 3 *c* showing the large nucleus filled with coarse granules, but showing no nucleolus; one, however, is seen in Fig. 3 *b. ncl.*; $\times 725$ diameters.
- FIG. 4.—Longitudinal section of the brain and suboesophageal ganglion, magnified 50 diameters, showing the relations between the two, and of the origin of the oesophageal commissure from the upper side of each ganglion, *i. e.*, from the back of the brain and the upper side of the suboesophageal ganglion.
- FIG. 5.—Enlarged view ($\times \frac{1}{2}$ B) of the suboesophageal ganglion of Fig. 6, Pl. x, showing the origin of the commissure to the first thoracic ganglion, and on the under side the three lobes (mandibular, maxillary, and labial), whence the nerves are sent to the mouth appendages. *mand. l.*, mandibular lobe; *max. l.*, maxillary, and *max. l'*, 2d maxillary or labial lobe; *com.*, commissure to suboesophageal ganglion.

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EDITORS' TABLE.

EDITORS: A. S. PACKARD, JR., AND E. D. COPE.

— The day is probably not distant when government aid for the protection of agriculturists against injurious plants and animals will be demanded as urgently as for geological, coast and land surveys. Let us glance briefly at the reasons why such aid becomes imperative. Until within three years no special attention had been given by Congress to these subjects; what little had been done by the botanist and entomologist connected with the Department of Agriculture being, from causes beyond their control, too slight to be worthy of mention. What had been done by the Government was much less than the efforts of several States, notably New York, Missouri and Illinois; these States having